

PATTERNS OF TEMPORAL VARIATION IN GOSHAWK REPRODUCTION AND PREY RESOURCES

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ABSTRACT.—To investigate whether Northern Goshawk (*Accipiter gentilis*) reproduction is food-limited, we evaluated the reproductive output from 401 goshawk breeding opportunities on the Kaibab Plateau, Arizona during 1999–2002. Concurrently, we estimated densities of 10 goshawk prey species (seven birds, three mammals) using distance sampling. We then assessed the relationship between goshawk productivity (number of fledglings produced) and prey density within and among years by relating the contribution of individual prey species and total prey density to goshawk productivity. We also estimated the proportion of total diet and biomass for each species that contributed $\geq 3\%$ of all prey items. Total prey density was highly correlated with variation in goshawk productivity ($r^2 = 0.98$, $P = 0.012$). Red squirrel (*Tamiasciurus hudsonicus*) density explained more variation in goshawk productivity than any other species ($r^2 = 0.94$, $P = 0.031$), but density could not be estimated for every predominant prey species in goshawk diets. However, only red squirrels had a positive and significant relationship to goshawk productivity in terms of frequency ($r^2 = 0.97$, $P = 0.014$) and biomass ($r^2 = 0.95$, $P = 0.033$). Northern Flickers (*Colaptes auratus*) and cottontail rabbits (*Sylvilagus* spp.), which contributed the greatest frequency and biomass, respectively, to goshawk diets, showed no relationship with goshawk productivity. Even though goshawks on the Kaibab Plateau have a diverse diet and will readily switch to alternate prey species, goshawk productivity showed significant interannual variation. Our results suggest that the magnitude of goshawk productivity was determined by total prey density and annual variation was driven by differences in the densities of critical prey species.

KEY WORDS: Northern Goshawk; *Accipiter gentilis*; diet; distance sampling; predator-prey dynamics; prey density; productivity.

PATRONES DE VARIACIÓN TEMPORAL DE LAS PRESAS Y DE LA REPRODUCCIÓN DE *ACCIPITER GENTILIS*

RESUMEN.—Para investigar si la reproducción de *Accipiter gentilis* se encuentra limitada por la disponibilidad de alimento, evaluamos el rendimiento reproductivo de 401 oportunidades reproductivas de estos halcones en Kaibab Plateau, Arizona, entre 1999 y 2002. Al mismo tiempo, estimamos las densidades de 10 especies de presas para los halcones (siete aves, tres mamíferos) utilizando el método de conteo con distancias variables. Luego determinamos la relación entre la productividad de los halcones (número de volantones producidos) y la densidad de presas dentro y entre años, relacionando la contribución de cada especie de presa y la densidad total de presas con la productividad de los halcones. También estimamos la proporción de la dieta total para cada especie que contribuyó más del 3% de todas las presas en la dieta. La densidad total de las presas se correlacionó fuertemente con la variación en la productividad de los halcones ($r^2 = 0.98$, $P = 0.012$). La densidad de la ardilla *Tamiasciurus hudsonicus* explicó la mayor parte de la variación en la productividad de los halcones con relación a las otras especies ($r^2 = 0.94$, $P = 0.031$), pero no se pudo estimar la densidad de cada especie de presa predominante en la dieta de los halcones. Sin embargo, sólo la ardilla *T. hudsonicus* presentó una relación positiva y significativa con la productividad de los halcones en términos de frecuencia ($r^2 = 0.97$, $P = 0.014$) y biomasa ($r^2 = 0.95$, $P = 0.033$). Las aves del género *Colaptes* y los conejos, que contribuyeron la mayor frecuencia y biomasa de la dieta de los halcones, respectivamente, no se cor-

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relacionaron con la productividad de los halcones. A pesar de que los halcones en Kaibab Plateau tienen una dieta diversa y pueden cambiar fácilmente a especies de presas alternativas, su productividad mostró una variación interanual significativa. Nuestros resultados sugieren que la magnitud de la productividad de los halcones fue determinada por la densidad total de presas y que la variación anual fue producida por las diferencias en la densidad de especies de presas críticas.

[Traducción del equipo editorial]

To understand temporal variation in population size, it is necessary to focus on the factors that limit demographic processes, such as reproduction and survival. Ultimately, the availability of essential resources within a habitat regulates population growth. Resource availability, specifically food, is hypothesized to be an important limiting factor of many raptor populations (Newton 1979). Variations in food supply often result in extensive fluctuations in population demographic parameters (Gotelli 1998, Newton 1998), but the mechanisms of food-limitation are difficult to quantify, especially in complex systems. Consequently, most information on the influence of food resources on population dynamics comes from correlations between reproduction and food abundance (Martin 1987).

The magnitude of the effects of food-limitation on reproduction is poorly understood, especially for predators with broad diets, such as Northern Goshawks (*Accipiter gentilis*). Goshawks regularly consume a variety of prey including ground and tree squirrels, rabbits, medium to large passerines, woodpeckers, and gallinaceous birds (Squires and Reynolds 1997). The diversity of prey in their diets ultimately depends on the abundance and availability of the local bird and mammal fauna, which varies geographically. In Canada, although goshawks regularly consumed several prey species (≥ 5), goshawk reproduction showed a strong functional response to only one species—snowshoe hare (*Lepus americanus*; Doyle and Smith 2001). In contrast, 14 species of birds and mammals regularly contributed to goshawk diets in the southwestern United States (Reynolds et al. 1992). This diet diversity may stabilize their breeding rates. When prey populations vary asynchronously, the ability of goshawks to switch between alternative prey species may result in less annual variation in reproduction than in areas where goshawks rely primarily on cyclic populations of a single prey species (Newton 1979).

Our objectives were to: (1) determine if prey resources limit the reproductive rates of goshawks with relatively diverse diets and (2) describe how

changes in prey populations may influence goshawk productivity (number of fledglings produced). If food is a limiting factor of goshawk productivity, then variation in the number of fledglings produced should be associated with fluctuations in prey resources. However, if there is a difference in the contribution of individual prey species, then goshawk productivity should respond to fluctuations in the densities of individual prey species. Finally, if the densities of important prey species vary in synchrony, then goshawk productivity should exhibit greater temporal variation. To explore these relationships we studied goshawk productivity and prey resources on the Kaibab Plateau, Arizona during 1999–2002.

STUDY AREA

The Kaibab Plateau is a large (95 × 55 km) forested island, surrounded by shrub-steppe desert, in northern Arizona. Steep slopes and escarpments form the eastern, southern, and western edges of the Kaibab Plateau and create a distinct boundary between the shrub-steppe desert at 1750 m elevation above sea level and the plateau (maximum elevation 2800 m). The northern edge of the plateau gradually descends to sagebrush desert, forming an indistinct boundary between the two landforms.

The study area (1285 km²) on the Kaibab Plateau included forests above 2182 m elevation on the North Kaibab Ranger District of the Kaibab National Forest. Four forest types dominated the study area: Pinyon-juniper (*Pinus edulis-Juniperus* spp.) woodlands occupied 106 km² at lower elevations, ponderosa pine (*Pinus ponderosa*) forests occupied 714 km² at mid-elevation zones, mixed conifer (*Abies concolor*, *Pinus ponderosa*, *Pseudotsuga menziesii*, *Picea engelmannii*) forests occupied 275 km² at the highest elevations, and quaking aspen (*Populus tremuloides*) forests occupied 112 km² interspersed among the other forest types (Joy 2002).

METHODS

Goshawk Productivity. We estimated annual goshawk productivity per territory in 1999–2002. A territory was defined as the area (approximately 11 km²) defended by a pair of goshawks during the breeding season (Reynolds et al. 2005). Because goshawks may use more than one nest within a territory among breeding years (Reynolds et al. 2005), all nest structures were visited annually in spring to determine the territory occupancy status. If an active nest (nest containing eggs or young) was not located within an existing territory, we conducted systematic surveys until we found an active nest or thoroughly

searched the entire territory, which required a minimum effort of 10 person-days (Reynolds et al. 2004). Each year, we also conducted surveys throughout the study area to locate territories not detected in previous years (Reynolds and Joy 2005). To determine nest status and fledgling production, all active nests were visited weekly throughout the breeding season. Goshawk offspring were counted in the nest 7–10 d prior to fledging or from the ground after fledging. Goshawk productivity was estimated annually as the mean number of fledglings produced per territory under study.

Prey Density. To obtain estimates of prey density, we conducted distance sampling (Buckland et al. 1993) along line transects from 1999–2002. Sixty 500-m transects were placed randomly throughout the study area within two strata defined by the forest types (mixed conifer, ponderosa pine) that occupied most of the study area. We established 30 transects per stratum and characterized each transect by its elevation, tree species composition, and tree density. Within a given year, we sampled each transect during three time periods that corresponded with specific goshawk reproductive stages: spring (28 May–24 June)–incubation/hatching stage, summer (25 June–22 July)–nestling stage, and late summer (23 July–14 August)–fledging stage. To reduce travel time between transects and to increase sampling efficiency, transects were grouped by location. Transects were sampled in groups of four per day, and the sampling order of groups was determined using a random number table. Daily sampling began 0.5 hr after sunrise and was completed within 3 hr. All transects were sampled by one observer (Salafsky) during the 4 yr of the study. Sampling was not conducted during inclement weather (rain, winds >20 kph) due to reduced probability of prey detection. Prey seen or heard during sampling were identified to species, and the perpendicular distance from the detected animal to the transect line was measured with a laser rangefinder (accurate to ± 1 m). Data were collected on 15 prey species common in goshawk diets on the Kaibab Plateau (S. Salafsky unpubl. data) and considered important components of goshawk diets in the southwestern United States (Reynolds et al. 1992).

Goshawk Diet. The species composition of goshawk diets was determined from prey remains (pelage, plumage, skeletal parts) that were collected from active goshawk nest sites during weekly visits throughout the breeding season. Prey remains were pooled by territory and date collected, identified to species, and paired to assess the minimum number of individuals consumed (Reynolds and Meslow 1984). The biomass contribution of individual prey was based on the published mass of each avian (Dunning 1993) and mammal (Hoffmeister 1986) species. All methods for quantifying raptor diets have inherent biases (Marti 1987). However, Kennedy (1991) reported that estimates of prey use were similar for prey remain, pellet, and direct observation methods of diet analysis for goshawks in New Mexico.

Data Analysis. We based goshawk productivity on the number of fledglings produced per territory under study. We classified territories based on ≥ 1 attempt to breed on the territory, the identity of the adult birds, and the average inter-territory distance (Reynolds et al. 2005). A high density of territories, a tendency of individuals to

retain the same territory for life, and a delayed age at first breeding (Wiens and Reynolds 2005) suggests that the breeding habitat on the Kaibab Plateau was saturated. This evidence combined with the observed patterns of territory occupancy for individual adults over a 14-yr period (S. Salafsky unpubl. data) indicated that goshawks occupied the territories, even when we found little evidence of birds present. By including all territories rather than only those that were confirmed “active” or “occupied,” we accounted for all potential breeding opportunities and the full range of variability in the reproductive quality of territories.

Variable distance sampling data were analyzed with program DISTANCE, Version 3.5 (Thomas et al. 1998). Reliable estimates of density from distance sampling depend on several critical assumptions: all individuals on the transect line were detected, all individuals were detected at their initial location, and all distances were measured accurately (Buckland et al. 1993). Data collection methods were designed to meet these assumptions. Because variable distance sampling uses a detection function that compensates for differences in detection probabilities among species, habitats, and distances from transects (Emlen 1971, Buckland et al. 1993), density estimates based on distance data are not confounded by factors affecting detectability and thus are representative of the true population size. Prey densities were estimated separately for mixed conifer and ponderosa pine to account for differences in detection probabilities among forest types. These estimates were then multiplied by the proportion of each forest type within the study area and added together to calculate prey densities for the entire study area. Annual density estimates were computed only for species with sufficient sample sizes. Total prey density was calculated as the sum of the individual prey densities for species with a sufficient number of detections. We stratified total prey density by sampling period within each year to estimate prey densities associated with goshawk breeding phenology.

We used the Tukey-Kramer adjustment for multiple comparisons of means to test for differences in goshawk productivity among years (PROC GLM, SAS Institute 1999). Z-statistics were used to test for differences in mean prey densities among years and sampling periods (Buckland et al. 1993). To control for Type I error, we only tested for differences in density between specific pairwise comparisons (e.g., years of highest and lowest density). To assess the relationship between goshawk productivity and prey density, we used linear regression (PROC REG, SAS Institute 1999), where annual goshawk productivity was the dependent variable, and estimates for individual prey species and summed over prey species were used as explanatory variables. Linear regression was also used to assess the relationship between goshawk productivity and prey species in the diet. In these regressions, annual goshawk productivity was the dependent variable and percent of total diet or biomass contribution for individual prey species were assessed as explanatory variables. We used an information-theoretic approach (Burnham and Anderson 2002) to identify the prey variables that explained the most annual variation in goshawk productivity per territory. *A priori* candidate models were developed to represent the potential effects of prey

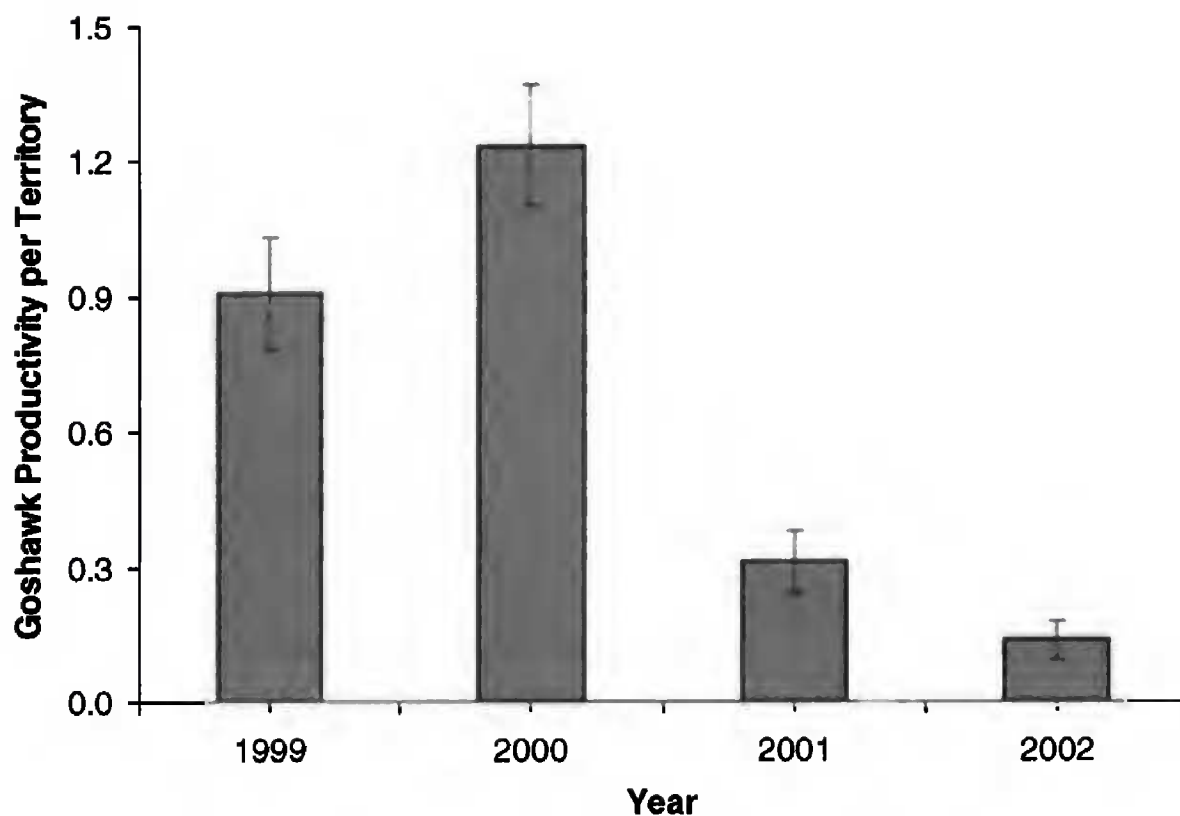


Figure 1. Mean number of Northern Goshawk fledglings produced per territory (\pm SE) on the Kaibab Plateau, Arizona, 1999–2002.

density on goshawk productivity. We hypothesized that goshawk productivity would be most strongly related to prey densities that contributed the most to goshawk reproduction. Competing models were ranked by their adequacy in explaining the variation in goshawk productivity using Akaike Information Criterion (PROC MIXED, SAS Institute 1999). To compare the relative importance of each prey species, we also used cumulative Akaike weights, which were calculated by summing the weights across all models that included the variable of interest (Burnham and Anderson 2002).

RESULTS

Variation in Goshawk Productivity. The number of goshawk territories used to estimate productivity was 97 in 1999, 98 in 2000, and 103 in 2001 and 2002 ($N = 401$). The proportion of territories with active nests was 54% in 1999, 58% in 2000, 28% in 2001, and 18% in 2002. Goshawk productivity ($\bar{x} \pm$ SE) varied among years ($F_{3,397} = 26.78$, $P < 0.001$) and ranged from 0.14 ± 0.04 fledglings produced per territory in 2002 to 1.23 ± 0.14 fledglings produced per territory in 2000 (Fig. 1). There was a significant decline ($F_{1,199} = 37.15$, $P < 0.001$) in goshawk productivity between 2000 and 2001 (Fig. 1).

Variation in Prey Density. Ten prey species had sufficient detections to estimate density: American Robin (*Turdus migratorius*), Clark's Nutcracker (*Nucifraga columbiana*), Downy Woodpecker (*Picoides pubescens*), golden-mantled ground squirrel (*Spermophilus lateralis*), Hairy Woodpecker (*Picoides vil-*

losus), Kaibab squirrel (*Sciurus aberti kaibabensis*), Northern Flicker (*Colaptes auratus*), red squirrel (*Tamiasciurus hudsonicus*), Steller's Jay (*Cyanocitta stelleri*), and Williamson's Sapsucker (*Sphyrapicus thyroideus*). We were unable to estimate densities for black-tailed jackrabbit (*Lepus californicus*), Blue Grouse (*Dendragapus obscurus*), chipmunk (*Eutamias* spp.), cottontail rabbit (*Sylvilagus* spp.), and rock squirrel (*Spermophilus variegatus*) due to low numbers of detections. Detection probability plots showed little evidence of heaping, measurement errors, and evasive movement prior to detection. Total prey density (\pm SE) varied annually and ranged from 2.22 ± 0.08 individuals ha^{-1} in 2001 to 3.96 ± 0.14 individuals ha^{-1} in 2000 ($z = 10.39$, $P < 0.001$). Density also varied significantly among years for most individual prey species (Table 1) including golden-mantled ground squirrel ($z = 2.18$, $P = 0.015$), Hairy Woodpecker ($z = -2.88$, $P = 0.002$), Kaibab squirrel ($z = 2.47$, $P = 0.007$), Northern Flicker ($z = 5.70$, $P < 0.001$), red squirrel ($z = 8.32$, $P < 0.001$), Steller's Jay ($z = 3.25$, $P < 0.001$), and Williamson's Sapsucker ($z = -2.78$, $P = 0.003$). Significant declines in prey densities were also observed between 2000 and 2001 for golden-mantled ground squirrel ($z = 2.18$, $P = 0.015$), Kaibab squirrel ($z = 2.47$, $P = 0.007$), Northern Flicker ($z = 2.62$, $P = 0.005$), and red squirrel ($z = 8.32$, $P < 0.001$), but only red squirrel

Table 1. Annual estimates of Northern Goshawk prey density ha^{-1} for American Robin (AMRO), Clark's Nutcracker (CLNU), Downy Woodpecker (DOWO), golden-mantled ground squirrel (GMSQ), Hairy Woodpecker (HAWO), Kaibab squirrel (KASQ), Northern Flicker (NOFL), red squirrel (RESQ), Steller's Jay (STJA), Williamson's Sapsucker (WISA), and all 10 prey species' densities combined (Total) on the Kaibab Plateau, Arizona, 1999–2002.

SPECIES	1999		2000		2001		2002	
	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE
AMRO	0.23	0.05	0.22	0.07	0.27	0.06	0.25	0.06
CLNU	0.05	0.02	0.05	0.02	0.04	0.01	0.11	0.04
DOWO	0.20	0.05	0.11	0.03	0.20	0.06	0.11	0.03
GMSQ	0.28	0.30	0.64	0.18	0.22	0.06	0.32	0.10
HAWO	0.09	0.03	0.05	0.02	0.23	0.06	0.17	0.04
KASQ	0.11	0.04	0.26	0.07	0.07	0.03	0.08	0.02
NOFL	0.58	0.08	0.77	0.09	0.48	0.06	0.20	0.04
RESQ	1.16	0.17	1.38	0.15	0.12	0.04	0.23	0.05
STJA	0.41	0.07	0.12	0.05	0.30	0.07	0.33	0.05
WISA	0.18	0.04	0.36	0.08	0.28	0.06	0.45	0.09
Total	3.29	0.19	3.96	0.14	2.22	0.08	2.24	0.09

density decreased by an order of magnitude (Table 1).

Prey density also varied by sampling period (Fig. 2). However, there were too few observations to accurately estimate density by sampling period for most individual prey species, so we report only total prey density by sampling period. Total prey density in the spring sampling period was highest in 2000, followed by 1999, 2002, and 2001 (Fig. 2). However, the decrease in density was only statisti-

cally significant between 1999 and 2002 ($z = 1.74$, $P = 0.041$), and 2002 and 2001 ($z = 6.58$, $P = 0.005$). The only significant decrease in total prey density between the late-summer sampling period of one year and the spring sampling period of the next occurred between 2000 and 2001 ($z = 6.58$, $P < 0.001$; Fig. 2).

Goshawk Diets. Goshawks on the Kaibab Plateau captured and consumed a wide diversity of prey. A total of 710 individual prey items consisting of 30

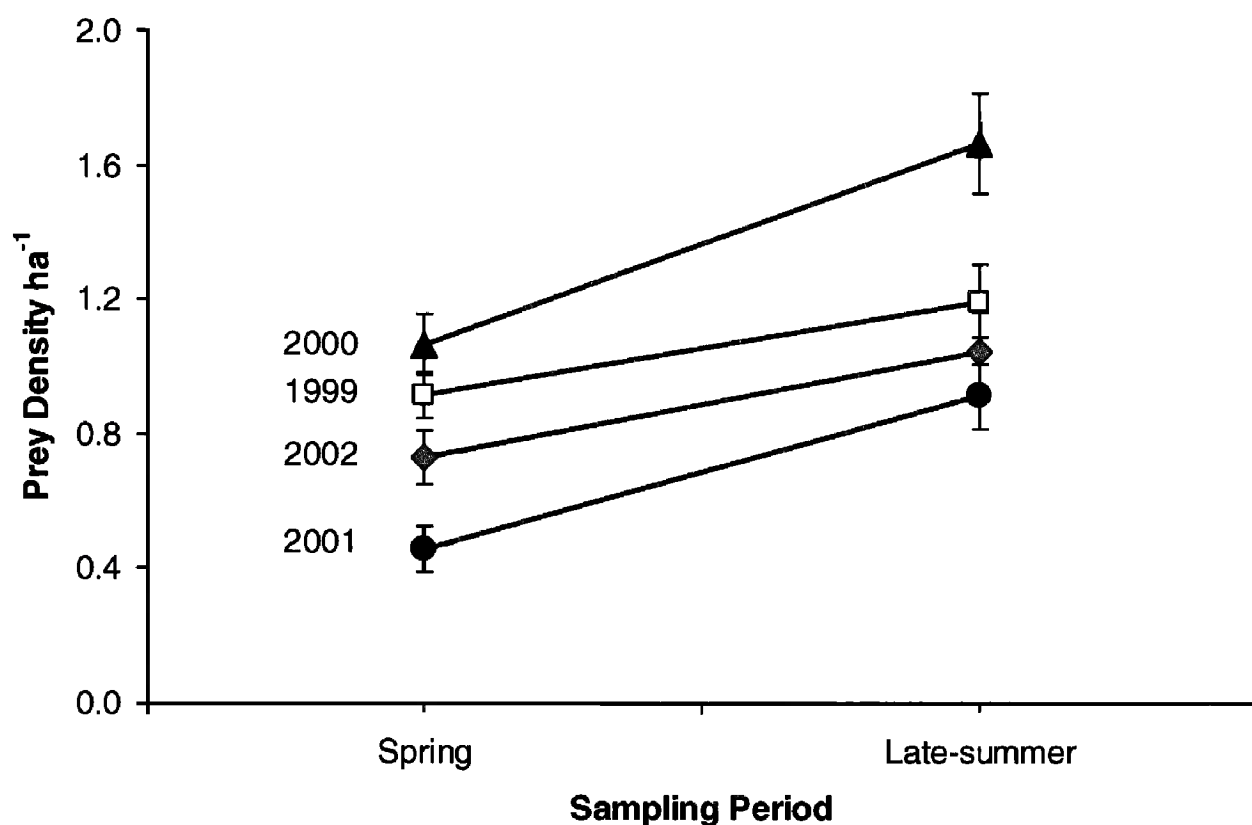


Figure 2. Total Northern Goshawk prey density estimates ha^{-1} (\pm SE) by sampling period on the Kaibab Plateau, Arizona, 1999–2002.

Table 2. Prey species each contributing $\geq 3\%$ of all items ($N = 710$) to Northern Goshawk diets in terms of percent frequency and biomass (kg), and their relationship to the number of fledglings produced per goshawk territory on the Kaibab Plateau, Arizona, during 1999–2002.

SPECIES	NO.	PERCENT FREQUENCY			PERCENT BIOMASS		
		R^2	P	R^2	P		
Black-tailed jackrabbit	23	3	-0.32	0.43	24	-0.36	0.40
Clark's Nutcracker	34	5	0.03	0.82	2	0.01	0.88
Cottontail rabbit	125	18	-0.13	0.64	42	-0.03	0.84
Kaibab squirrel	40	6	-0.05	0.78	13	0.02	0.87
Northern Flicker	141	20	0.87	0.07	8	0.87	0.07
Red squirrel	87	12	0.97	0.01	7	0.95	0.02
Steller's Jay	88	12	-0.09	0.70	4	0.04	0.81

species were collected from nest areas during 1999–2002. Seven species each contributed $\geq 3\%$ of all prey items collected in terms of percent frequency (Table 2). In descending order of percent of total diet, the most common prey items were Northern Flickers, cottontail rabbits, red squirrels, Steller's Jays, Kaibab squirrels, Clark's Nutcrackers, and black-tailed jackrabbits. The descending order of species biomass contribution to goshawk diets was: cottontail rabbits, black-tailed jackrabbits, Kaibab squirrels, Northern Flickers, red squirrels, Steller's Jays, and Clark's Nutcrackers (Table 2). The mean number of prey items per fledgling was 1.8 in 1999, 2.3 in 2000, 5.1 in 2001, and 7.6 in 2002. In contrast the mean biomass of prey items

per fledgling was 0.8 kg in 1999, 0.6 kg in 2000, 2.3 kg in 2001, and 2.8 kg in 2002.

Goshawk Productivity and Prey Resources. We found a strong positive relationship ($r^2 = 0.98$, $P = 0.012$) between total prey density and goshawk productivity from 1999–2002 (Fig. 3). Although annual goshawk productivity was highly correlated with prey density in the spring sampling period ($r^2 = 0.70$, $P = 0.163$), summer sampling period ($r^2 = 0.75$, $P = 0.131$), and late-summer sampling period ($r^2 = 0.79$, $P = 0.112$), annual prey density accounted for more of the variation in goshawk productivity. Based on regression models for each prey species, only red squirrel density had a significant and positive relationship to goshawk produc-

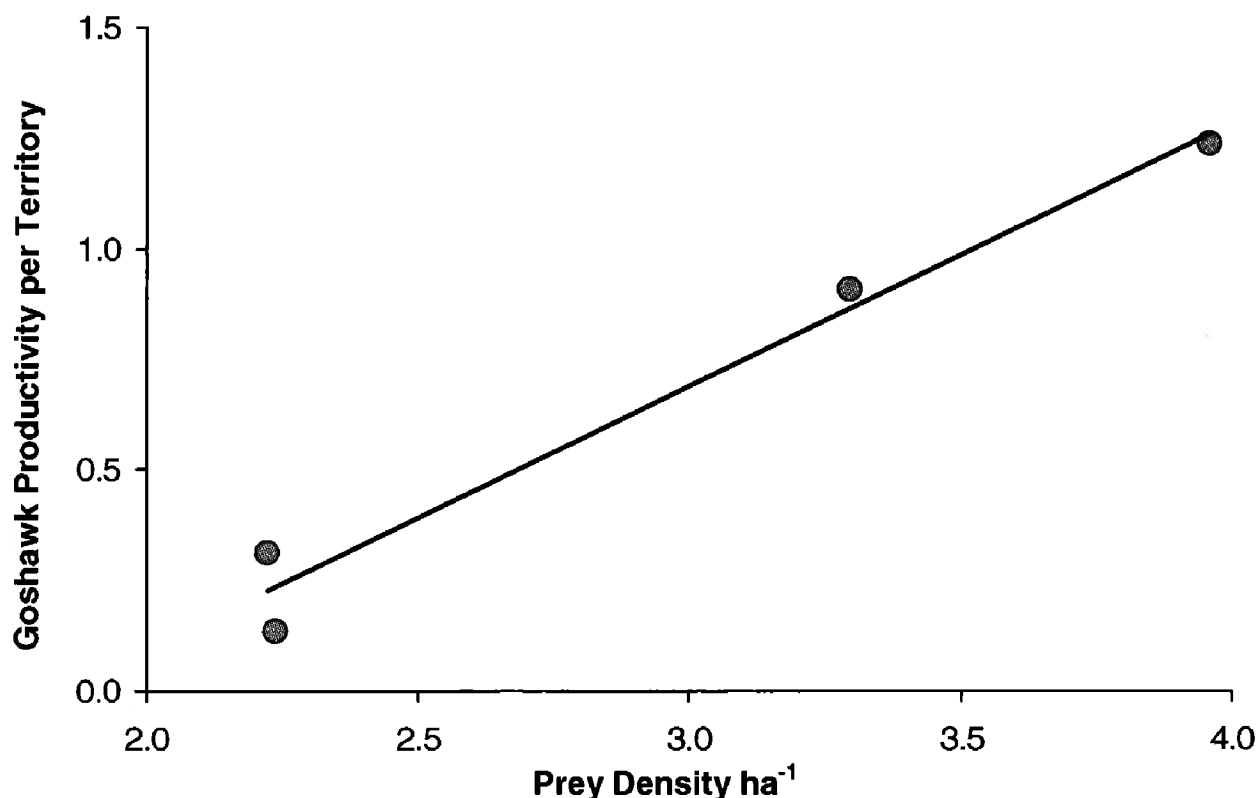


Figure 3. The relationship between total prey density ha^{-1} and the mean number of Northern Goshawk fledglings produced per territory on the Kaibab Plateau, Arizona, 1999–2002.

Table 3. Top 10 models for mean number of Northern Goshawk fledglings produced per territory on the Kaibab Plateau, Arizona, 1999–2002. Models are ranked based on Akaike's Information Criteria (AIC) and include model covariates, number of parameters (K), AIC differences (Δ AIC) and Akaike weights (w_i).

MODEL	AIC	K	Δ AIC	w_i
Total prey species	1134.80	3	0.00	0.70
Red squirrel	1137.70	3	2.90	0.16
Mammal prey species	1138.10	3	3.30	0.13
Northern Flicker	1144.20	3	9.40	0.01
Total prey in late-summer	1149.50	3	14.70	0.00
Hairy Woodpecker	1150.80	3	16.00	0.00
Total prey in summer	1152.20	3	17.40	0.00
Kaibab squirrel	1154.20	3	19.40	0.00
American Robin	1155.40	3	20.60	0.00
Total prey in spring	1156.90	3	22.10	0.00

tivity ($r^2 = 0.94$, $P = 0.031$). Red squirrel was also the only species that had a significant and positive relationship to goshawk productivity for percent of diet ($r^2 = 0.97$, $P = 0.014$) and biomass ($r^2 = 0.95$, $P = 0.024$; Table 2). The densities of mammal prey species ($r^2 = 0.94$, $P = 0.033$) explained more of the variation in goshawk productivity than avian prey species ($r^2 < 0.01$, $P = 0.949$).

Our model selection results showed that total prey density was clearly the top model (Table 3). This model, which included an annual summation of all prey species' densities, received >70% of the Akaike weight across the model set (Table 3) and was more than four times as likely as the next best model. The only single species models with some weight of evidence included those for red squirrel and Northern Flicker (Table 3). However, the red squirrel density covariate had a higher cumulative Akaike weight (99%) than Northern Flicker (71%). All other models based on individual prey species, avian density, and models of total prey density by sampling period had minimal support and failed to explain variation in goshawk productivity (Table 3). When we compared only the models with total prey density by sampling period in a separate analysis, total prey density summed over all sampling periods was selected as the best model (AIC = 811.10, K = 3, Δ AIC = 0.00, $w_i = 0.93$). All other models, including the model with the difference in prey density between late-summer and the successive spring (AIC = 873.00, K = 3, Δ AIC = 61.90, $w_i = 0.00$) and the lowest ranked model with late-summer prey density from the prior year (AIC = 883.60, K = 3, Δ AIC = 72.50, $w_i = 0.00$), were not supported by the data.

DISCUSSION

A short-term observational study cannot provide a strong basis for estimating the causal relationship between prey resources and annual goshawk productivity. Thus, our study only established a strong association between variation in prey resources within the study area and goshawk productivity. Because fluctuations in other limiting factors (e.g., climate) may have coincided with changes in prey resources, we cannot identify the factors ultimately responsible for variation in goshawk productivity. However, if the patterns we observed between prey resources and goshawk productivity were supported by experimental studies that established a relationship between food-supply and goshawk reproduction, then it would be reasonable to infer that prey resources may be an important limiting factor of goshawk reproduction on the Kaibab Plateau.

During 1999–2002 we observed high temporal correlations between goshawk productivity and annual prey density; changes in goshawk productivity paralleled changes in prey density. Total prey density, in addition to the proportion of active goshawk nests and mean number of fledglings produced, was high in 1999 and 2000 and low in 2001 and 2002. Therefore, it appears that goshawk reproduction on the Kaibab Plateau responded to inter-annual increases in prey density. Several other studies have also found close ties between measures of goshawk reproduction and the relative abundances of prey (Huhtala and Sulkava 1981, Doyle and Smith 1994, Keane 1999). Further, goshawk studies that experimentally manipulated food-supply found supplemental food may have in-

fluenced goshawk productivity by increasing nestling survival when background prey-levels were low (Ward and Kennedy 1996, Dewey and Kennedy 2001). Thus, we suggest that the number of goshawk fledglings produced may be influenced by fluctuations in prey density.

On an annual basis, the reproductive responses of goshawks depend on the abundance of prey during critical time periods. Low food resources may manifest through failure to lay eggs, smaller clutches, and reduced survival of young (Newton 1998). The abundance of prey may be an important determinant of the "decision" to breed. Goshawks initiate breeding before most prey species reproduce, so the density of prey during the incubation period is likely similar to prey levels prior to egg-laying. On the Kaibab Plateau, prey densities during the incubation stage were similar in 1999 and 2002, yet goshawk productivity was six times higher in 1999. In addition, although there was a significant increase in prey density during the incubation period between 2001 and 2002, goshawk productivity changed little between these years, suggesting that below a density of ca. 0.8 prey ha⁻¹, fewer fledglings are produced. However, prey density levels prior to egg-laying may alter the threshold effects of prey density on goshawk productivity through physiological constraints. Assuming our density estimates represented true population size, the difference in prey density between late-summer and the next spring should reflect prey density levels prior to egg-laying. The large decline we observed in prey density between August 2000 and May 2001 indicated that there was substantial overwinter mortality for prey species. The lower prey numbers prior to egg-laying may have affected the ability of females to accumulate sufficient reserves to produce eggs in 2001.

Our results suggest there is a difference in the contribution of individual prey species to goshawk reproduction. Red squirrel density and their percent frequency and biomass contribution to goshawk diet accounted for more variation in goshawk productivity than any other species. Although rabbits contributed the majority of biomass to goshawk diets (>66%), goshawk reproduction was lower in most years when rabbits contributed the greatest proportion of biomass to the diets. Further, in "poor" goshawk reproductive years (2001, 2002), the number of prey items and total biomass per fledgling was twice as high as in "good" reproductive years (1999, 2000). The difference in the

apparent influence of individual prey species is likely a result of encounter rates with goshawks. Goshawks are opportunists and will presumably attempt to capture whatever prey species are readily available. However, the limited distributions or different activity patterns of some prey species decreases the probability that diurnal goshawks will encounter them while foraging. Jackrabbits are less common in upper elevation forests, and although cottontails are widely distributed across the study area, they are crepuscular (Hoffmeister 1986). In contrast, red squirrels are among the heaviest of the diurnal prey species, with a wide distribution across the study area (Salafsky 2004). Red squirrels do not hibernate, which likely increases their importance to goshawks, particularly prior to egg-laying. However, the importance of other prey species may vary with the spatial distribution of goshawk territories relative to the spatial distribution of prey habitats. For example, goshawks with territories located primarily within lower elevation forests may rely more heavily upon jackrabbits.

In our study, goshawk productivity on the Kaibab Plateau was more closely associated with variation in mammal density than in avian density. Goshawks may consume more mammals than birds in some areas due to the availability and sizes of local prey species (Zachel 1985, Widén 1987, Doyle and Smith 1994). Similar to our study, Boal and Mannan (1994) and Reynolds et al. (1994) found that goshawks on the Kaibab Plateau consumed a higher proportion of mammalian prey. Other goshawk studies conducted in northern latitudes identified a strong link between goshawk reproductive rates and cyclical variation in hare abundance (McGowan 1975, Doyle and Smith 2001). Because annual variations in predator reproductive rates are greatest among species with limited diets that are dominated by cyclic prey (Newton 1979), goshawks on the Kaibab Plateau may be subject to more marked variations in productivity due to their reliance on prey species with fluctuating densities.

Goshawks have the ability to switch to alternate prey when the densities of essential prey species are reduced (Doyle and Smith 1994). However, if different prey species' populations decline simultaneously, then the opportunities for goshawks to switch to alternative prey species are limited. The densities of golden-mantled ground squirrels, Kaibab squirrels, Northern Flickers, and red squirrels declined significantly between 2000 and 2001. Further, these species contributed >39% of all prey

items to goshawk diets. Parallel fluctuations in annual densities of important prey species may result in potentially "poor" and "good" years of prey resources. Thus, it may be that the collective density of the entire prey community influences the magnitude of variation in goshawk productivity on the Kaibab Plateau.

In summary, our results indicate that prey density is an important limiting factor of goshawk productivity. Although the temporal correlations between goshawk productivity and prey resources were consistent over time, other factors may have varied with prey density and limited goshawk reproduction in our study. Synchronous declines in prey species' densities suggests that landscape-level factors acting at broad spatial scales, such as climate, may interact with prey abundance to limit goshawk productivity. Because unfavorable weather conditions may have a greater effect on goshawk productivity when prey resources are already low, it is important to study the relationship between goshawk productivity and prey density over long time periods and variable environmental conditions.

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